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Wüest, Rafael O ; Boucher, Florian C ; Bouchenak-Khelladi, Yanis ; Karger, Dirk N ; Linder, H Peter

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Short running title:
Diversity dynamics in the Cape hotspot

Authors:
Rafael O Wüest[1,*,†], Florian C. Boucher[2,3,*], Yanis Bouchenak-Khelladi[4], Dirk N. Karger[1], H. Peter Linder[4]

[1] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Forest Resources and Management, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland
[2] Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland, 7602 South Africa
[3] Université Grenoble Alpes, CNRS, Laboratoire d'Ecologie Alpine (LECA), 2233 rue de la Piscine, FR-38000 Grenoble, France
[4] Institute for Systematic and Evolutionary Botany, University of Zürich, 8008 Zürich, Switzerland
* these authors contributed equally
[†] corresponding author: rafael.wueest@gmail.com

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ABSTRACT

Aim: Fragmented distributions should show immigration and diversification dynamics consistent with the predictions of island biogeography theory. We test whether this applies to the fragmented Cape fynbos vegetation.

Location: Southern Africa, Cape Floristic Region (CFR)

Taxon: Angiosperms, Restionaceae (restios)

Methods: We used a large occurrence dataset and environmental layers to characterize an existing regionalization and the intervals between the regions ecologically and spatially. We extended the available phylogeny for restios and inferred their historical biogeography using models implemented in BioGeoBEARS. We then measured the relative contribution of immigration and *in situ* speciation to the species richness of each region within the CFR. We used standard statistical methods to test the predictions of the island biogeography theory.

Results: The area and environmental heterogeneity of the seven regions of the CFR are positively correlated with *in situ* speciation rate. Furthermore, more isolated areas, and areas colonized more recently, have proportionally higher immigration rates, and more central and older areas proportionally higher *in situ* speciation rates.

Main Conclusions: The variation in immigration and diversification dynamics among the regions within the CFR is extensive and consistent with the archipelago model of island biography theory. This dynamic may contribute significantly to the diversity of the Cape flora. Such a model could be generally useful for understanding the generation and maintenance of diversity in biodiversity hotspots, and may even scale up to explain continental biodiversity.

KEYWORDS

Cape flora, dispersal, hotspot, immigration – diversification dynamics, island biogeography theory, metapopulation, Restionaceae, semi-permeable barriers

INTRODUCTION

A rich body of theory has been developed over the decades to explain the processes that generate diversity in a fragmented system. Sewall Wright (1943) first contributed his island model in his original analysis of genetic differentiation under isolation by distance. The equilibrium island biogeography theory of MacArthur and Wilson (1967) constitutes another important advance, as it predicts the relative contributions of immigration and extinction in generating diversity in island(-like) systems. This theory was expanded to include speciation (Heaney, 2000; Rosindell & Phillimore, 2011) island ontogeny (Whittaker, Triantis, & Ladle, 2008), and the effect of archipelagos (Gascuel, Laroche, Bonnet-Lebrun, & Rodrigues, 2016). Metapopulation theory (Hanski, 2001) was inspired by island biogeography theory, but mainly focused on the aspects of fragmentation: a meta-population is defined as a set of isolated populations on discrete habitat fragments, not all of which are occupied by the focal taxon, as such very similar to islands but without a mainland. Hanski and collaborators in a series of seminal papers used metapopulation theory to explore the impact of fragmented ranges on extinction and speciation rates (Hanski, Mononen, & Ovaskainen, 2011). Central to these theories is the idea that diversity scales differently with area in fragmented compared to continuous habitats, and that this impacts the rates of the three processes that generate diversity: speciation, extinction and immigration (Table 1). Fragmentation should increase both the extinction rate (at least within the fragments; Rybicki & Hanski, 2013), especially if the fragments are small, and speciation rate (Gascuel et al., 2016). Total net diversification rate should be maximal when the barriers separating the areas are semi-permeable, with an intermediate dispersal rate leading to the highest diversity. The speciation rate within a fragment should increase with its area size and the ecologically heterogeneity (Heaney, 2000; Kisel & Barraclough, 2010; Whittaker et al., 2008). Immigration should be more important in less isolated areas (Stuessy, 2007).

Many species rich areas are fragmented, this can be by water as in the Philippines (Brown et al., 2013), edaphically as in West Australia (Hopper, 1979), or elevationally as sky islands in the Northern Andes (Madriñán, Cortés, & Richardson, 2013). These resemble the collection of islands in an archipelago (MacArthur & Wilson, 1967), or the patchy habitats typically used in meta-population theory. Hence, the island biogeographic model and metapopulation theory provide hypotheses that predict the relative contribution of immigration and in-situ speciation to the diversity in geographically fragmented areas, if the age, size, isolation, and heterogeneity of the fragments is known.

The Cape flora in southern Africa, with over 9’400 species in 90’800 km^2 (Goldblatt & Manning, 2000), is one of the global biodiversity hotspots (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). The evolution and maintenance of this remarkable diversity has attracted much research on the sources of the lineages (Galley & Linder, 2006; Verboom et al., 2014), the age of the radiations that built the diversity (Linder, 2003; Onstein,

Carter, Xing, Richardson, & Linder, 2015; Verboom et al., 2009; Verboom et al., 2014), the potential speciation mechanisms that drove this diversification (Johnson, 1996; Linder, 1985; Schnitzler et al., 2011), and the processes that facilitate the maintenance of diversity (Slingsby & Verboom, 2006). Although it has long been known that the "fynbos" flora is fragmented into centres of endemism (regions), separated by barriers with a different vegetation type (*i.e.* renosterveld; Weimarck, 1941), the impacts of fragmentation on speciation and immigration rates, mediated by the strength of barriers, the size and age of first colonization of the regions, and their heterogeneity, have not received much attention. If we consider the Cape flora as an archipelago, then we can use island biogeography theory and its extensions to predict the variation in richness among its fynbos fragments based on each fragment's size, environmental heterogeneity, age (Price et al., 2018) and position in the archipelago (Gascuel et al, 2016).

Table 1 *Theoretical expectations from island biogeography and meta-population theory on the relationship between processes generating diversity in each fragment (i.e., a habitat island), and fragment attributes. Relations in brackets are expected to be weak.*

Process	Size	Ecological heterogeneity	Age	Isolation
Immigration	(Positive)[a]	(Positive)[b]	Negative[c]	Negative[d]
Diversification	Positive[e]	Positive[f]	Positive[g]	Neutral
Relative importance of diversification over immigration	Positive	Positive	Positive	Positive

[a] (MacArthur & Wilson, 1967), [b] (Whittaker et al., 2008), [c] (Whittaker et al., 2008), [d] (MacArthur & Wilson, 1967), [e] (Heaney, 2000; Kisel & Barraclough, 2010; Losos & Schluter, 2000), [f] (Losos & Schluter, 2000; Whittaker et al., 2008), [g] (Heaney, 2000; Losos & Schluter, 2000)

Here, we use the theory and its hypotheses (Table 1) to predict the relative importance of alternative biogeographic processes (*i.e.* immigration versus *in situ* speciation) in determining the observed diversity patterns in the African Restionaceae (hereafter "restios"). The monophyletic restios dominate the "fynbos", the most species-rich vegetation of the Cape flora (Rebelo, Boucher, Helme, Mucina, & Rutherford, 2006), ecologically. Furthermore, with 350 species restios constitute one of the largest clades in the flora (Linder, 2003), and as such are suitable for exploring patterns and processes within this flora. We first postulate that in the Cape the ecological suitability of habitat in the barrier region might be more important than simply the width of the barrier. Consequently, we predict that biogeographic models in which dispersal is based on ecological suitability will outperform models that only take into account geographic distance. Secondly, we test whether the predictions of the island biogeography theory (Table 1) apply to the restios: that fragment size, ecological heterogeneity, age of first colonization and isolation are positively correlated with the relative importance of *in situ* speciation over immigration in building diversity. We use deviations from the predictions to explore alternative explanations of the diversification of the Cape restios.

MATERIALS AND METHODS

Phylogeny and distribution data

We inferred a chronogram of the restios from published plastid sequence data (*atpB-rbcL* (320 species), *trnK-matK* (309 spp), *trnL-F* (329 spp), *psbA-trnH* (156 species), and *rpl32-trnL* (49 species) representing 335 species, and added five species for which we generated DNA sequences of *atpB-rbcL* (5 sequences), *trnK-matK* (5 sequences), *trnL-F* (5 sequences) and *psbA-trnH* (4 sequences; see details in Table S1 in Supporting Information). Thus, we sampled a total of 340 restio species and added two Australasian Restionaceae, *Baloskion tetraphyllum* and *Sporodanthus tasmanicus,* as outgroups. Twenty-two restios were dropped from the tree, as their identification were not secure, or they occurred outside the study region, leaving 318 species in the dataset. The phylogenetic inferences and molecular dating procedures follow Bouchenak-Khelladi and Linder (2017). Results were summarized using a maximum clade credibility (MCC) tree, which we used for testing different models of ancestral area optimizations. For estimating parameters of the best model we used 100 trees sampled randomly from the posterior tree distribution after burnin.

Occurrence records of restios were compiled from available herbarium records (largely the Bolus Herbarium of the University of Cape Town and the Compton Herbarium of the South African National Biodiversity Institute), as well as 916 relevés from across the Cape Floristic Region (CFR). This dataset was critically edited, and all records with potentially dubious identifications and incorrect locality data removed, so that it can be

regarded as being "clean", allowing us to use all datapoints, constituting a set of 12'903 data points (Fig. 1). In the final analysis 318 species with both spatial and phylogenetic information were included. Both phylogenetic trees as well as the occurrence data are available on the DRYAD digital repository upon acceptance of the manuscript (http://dx.doi.org/XXXX).

Climatic and geological data

The climate data used in this analysis are based on CHELSA 1.2 (Karger et al., 2017), available at www.chelsa-climate.org/downloads at a spatial resolution of 30arc-sec (ca. 1x1km). We selected a set of bioclimatic variables with additional climatic aggregations derived from monthly mean-, maximum-, and minimum temperatures, as well as monthly precipitation. A full set of the variables used and the methodology is described in Appendix S1, Table S2 and available on the DRYAD digital repository upon acceptance of the manuscript (http://dx.doi.org/XXXX).

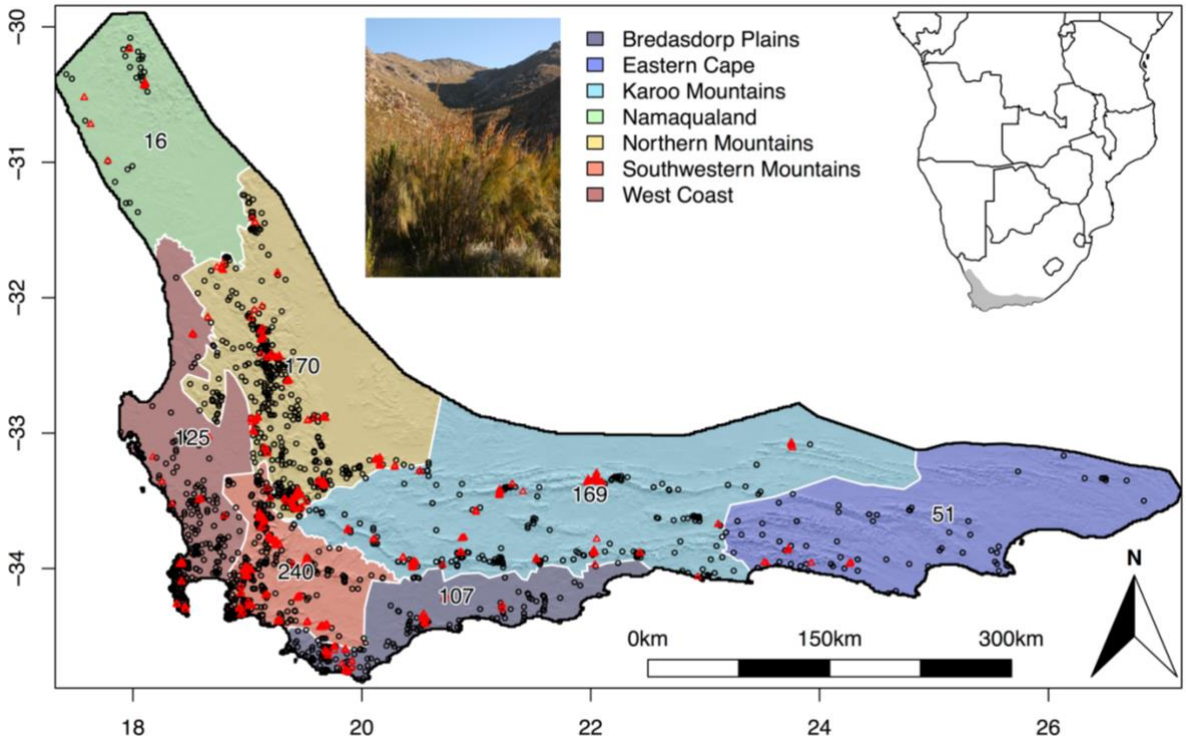

Figure 1 *Overview of the study area (Cape Floristic Region), with the map inset showing sub-equatorial Africa and the study area in grey. The regions used for this study are coloured according to the figure legend, and the numbers in each region depict current restio species richness. Black dots indicate restio occurrences, red triangles locations of relevés. The image is of Cannomois grandis, in the Great Swartberg (photo credit: Peter Linder).*

Geological information was obtained from the South African Council for Geoscience (downloaded in January 2018 from http://www.geoscience.org.za). These data describe the geology of South Africa at a resolution of 1:1'000'000 using 496 classes. We simplified these classes to consist of six major geological classes: calcrete, granite, recent sand, silcrete, sandstones, shale, others (including water-bodies and classes outside the CFR; details of conversion in Table S3). A shapefile with the geologic information for the CFR is available on the DRYAD digital repository upon acceptance of the manuscript (http://dx.doi.org/XXXX).

Modeling habitat suitability

We used species distribution models to estimate the potential suitability of habitats for restios of the CFR. In an ensemble approach, we used four statistical models to relate restio occurrence with climatic and geological information. Appendix S2 outlines how we selected the climatic variables and the details of fitting the four models: GLM (Nelder & Wedderburn, 1972), GAM (Hastie & Tibshirani, 1990), Random Forest (Breiman, 2001) and MaxEnt (Phillips, Anderson, & Schapire, 2006) in R (R Development Core Team, 2017). We averaged the predicted habitat suitability values from the four models to obtain an ensemble habitat suitability and transformed these averaged values into a binary presence-absence map by using a threshold that optimizes the True Skills Statistic (TSS; Allouche, Tsoar, & Kadmon, 2006) of observed versus predicted presence and absence across the entire restio dataset.

Delineation of regions

The three major regionalization studies of the Cape flora (Weimarck, 1941; Oliver, Linder, & Rourke, 1983; Bradshaw, Colville, & Linder, 2015;) resulted in different groupings. However, analyses of only restios (Linder & Mann, 1998; Linder, 2001; Moline & Linder, 2006), using presence data by quarter-degree square or natural regions, located a set of congruent regions, which we use here. These nine regions (Namaqualand, Northern Mountains, West Coast, Southwestern Mountains, Cape Peninsula, Bredasdorp Plains, Langeberg Mountains, Swartberg Mountains and Eastern Cape) are largely separated by gaps in the restio distribution range, which are correlated with either / or low rainfall, high summer temperatures and heavy clayey soils, habitat variables not generally associated with restios or fynbos. Preliminary tests showed that ancestral biogeographic reconstructions would not run in reasonable time when using nine regions, which corresponds to 512 possible ancestral ranges (*i.e.* single regions plus all possible combinations of them). We thus combined some regions by calculating floristic distances (using the Sørensen index) between the nine initial regions based on their restio species composition and then clustering them using the unweighted pair group method with arithmetic mean. Based on the clustering result we grouped the West Coast with the Cape Peninsula (=West Coast) and the Langeberg mountains with the Swartberg/Karoo region (= Karoo Mountains). The Northern and

Southwestern Mountains also had very similar floristic compositions but we preferred to keep them as separate regions as both of them are large and harbour extremely high restio richness. This left us with seven regions (Fig. 1), reducing the number of possible ranges to 128.

Characterizing isolation, size, and environmental heterogeneity of regions

We used two approaches to quantify the isolation between the regions. The first approach quantifies isolation by geographical distance. For this, we restricted the regions to contain only suitable restio habitat using the binary presence-absence map, and calculated the smallest geographical distance between suitable habitat patches among the regions (D_{geo}). The second approach quantifies isolation by calculating ecologically informed distances (D_{eco}). Habitat suitability can be used to assess ecologically informed distances between patches in a landscape by assuming that the resistance to move through a landscape inversely scales with habitat suitability. We used the ensemble habitat suitability map to estimate resistance to restio dispersal through the CFR using CIRCUITSCAPE 4.0.5 (McRae, Shah, & Mohapatra, 2014). CIRCUITSCAPE uses circuit theory to estimate connectivity between patches or regions, where voltage and resistance (or its inverse: conductance) determine electrical current (McRae, 2006; McRae, Dickson, Keitt, & Shah, 2008). We estimated pairwise resistance as an analog of isolation between regions by supplying a region identification layer and the habitat suitability as conductance layer.

The size of each region was calculated by limiting each region to only the habitat suitable for restios (using the binary presence-absence map). We performed a principal component analysis (PCA) on the climatic variables used in modeling habitat suitability to quantify environmental heterogeneity. The first five components of the PCA explained >75% of the climatic variation in the CFR. Therefore, we calculated the standard deviation of the PCA-scores within each region for the first five components and summed these to obtain region-specific heterogeneity.

Historical biogeographic reconstructions

Ancestral ranges were reconstructed using the Dispersal-Extinction-Cladogenesis model (Ree & Smith, 2008) as implemented in the 'BioGeoBEARS' R package (Matzke, 2013). We did not include founder-event speciation as a possible biogeographic process as its statistical properties have recently been criticized (Ree & Sanmartín, 2018). Ancestral ranges containing up to all seven regions were allowed because two species, *Restio capensis* and *R. sieberi,* are very widespread across the CFR and currently occur in all seven regions. However, we forbid disjunct ancestral ranges because this situation does not occur in extant restios, and this reduced the number of possible ranges to 100. Three models of dispersal between regions were compared: (i) equal dispersal rates between any two regions (D_0 model), (ii) dispersal rates that vary exponentially as a function of the geographical distance between two regions (D_{geo} model) and (iii) dispersal rates that vary exponentially as a function of the ecologically informed distance between two regions (D_{eco} model). In the two

last models, dispersal rate between two regions *i* and *j* was thus expressed as $D_{i,j}=d*M_{i,j}^{x}$, where *d* is a general scaling parameter for dispersal rates, *M* is the matrix of distances (geographical or ecologically informed) between regions and *x* is a parameter determining the shape of the relationship between distance and dispersal rate (Matzke, 2013).

Statistical comparison of these three models was done using the Akaike information criterion (AIC), based on maximum-likelihood estimation on the MCC tree only. Preliminary tests showed us that optimizing both *d* and *x* is difficult. Consequently, when fitting models D_{geo} and D_{eco} on the MCC tree we ran four independent optimizations starting from different initial values and then retained the one with the highest likelihood. We then estimated parameters of the best fitting model on 100 phylogenetic trees randomly sampled from the posterior of our phylogenetic analysis and used it to simulate past biogeographic scenarios in restios, using stochastic mapping (Dupin et al., 2017). In order to account for both the stochasticity of biogeographic range evolution and phylogenetic uncertainty, we ran 100 stochastic mappings for each of 100 posterior phylogenetic trees. Finally, for each of these stochastic mappings we recorded the number of dispersals in and out of each region, and from that calculated the relative contributions of immigration versus *in situ* speciation to the species richness of each region. The relative contribution of speciation in a given region was calculated as the number of *in situ* speciation events over the species richness of the region, and the relative contribution of immigration was calculated as 1 minus the relative contribution of speciation. However, the role of extinction, locally or across the whole CFR, was ignored. Finally, we also recorded for each stochastic mapping the age of the first arrival of restios in each region, which we refer to as the age of colonization of each region.

Statistical analyses

An assumption underlying our predictions is that our regions are biologically meaningful. We tested this assumption by calculating species turnover between restio communities within compared to between regions. If regions are biologically distinct, we expect greater compositional turnover between than within regions. We calculated pairwise turnover between all relevés in our database (n=916) using the Simpson dissimilarity index (Simpson 1943). Using matrices of pairwise compositional turnover leads to nonindependence in the data, so we used the 'MCMCglmm' R package (Hadfield, 2010) to fit a linear mixed effect model that accounted for this nonindependence. Compositional turnover is expected to increase with geographic distance, which we also included as a predictor. Such a model allows to test if compositional turnover is greater between regions compared to among regions, while controlling for the effect of geographical distance. Convergence of MCMC chains was confirmed by examining trace plots and inspecting autocorrelation of MCMC samples.

We tested our predictions on how the relative contributions of *in situ* speciation and immigration to regional diversity relate to isolation, age, size and heterogeneity of each

region by means of linear models in R while transforming the two responses with a logit link, because they are defined as proportions. For both *in situ* speciation and immigration we used the mean of the repetitions across phylogenetic trees and stochastic mappings.

RESULTS

Phylogenetic tree, regions and ancestral area reconstructions

The MCC tree topology and mean age estimates (Fig. S1) are very similar to the chronogram produced by Bouchenak-Khelladi and Linder (2017) with a Restionoideae crown age of 68.6 Ma (95% HPD: 56.3-77.4). The tree is well supported, with a posterior probability > 0.95 for 247 of the 337 nodes (73%). The major clades (tribes Willdenowieae and Restieae), and most of the genera are retrieved with strong support. The persistent phylogenetic problems with generic delimitations in the Willdenowieae and the fragmentation of the genus *Restio* are also retrieved. The compositional turnover between plots within a region, corrected for distance, is significantly less than the turnover between plots between regions (Table S4).

Among the three dispersal models that we compared on the MCC tree, ecologically informed distances received by far the best fit (ΔAIC=38.5 with the D_{geo} model and ΔAIC=51.6 with the D_0 model; Table 2). When fitted over the MCC tree, this model gave a rather unambiguous estimation of restios' ancestral biogeographic areas, with 174 out of the 317 internal nodes (55%) in the tree receiving more than 50% marginal likelihood for one given biogeographic range (out of the 128 possible ranges). Parameter estimates of this model over the 100 trees from the posterior were d=0.041±0.0075 (mean±sd) and x=-0.31±0.022, which indicates that the dispersal rate between two regions decreases rather smoothly with the ecologically informed distance between them.

Table 2 *Akaike information criteria (AIC) of the three fitted BioGeoBEARS models comparing barrier types for restios in the Cape Floristic Region. It is possible to condition dispersal in BioGeoBEARS on some distance measure. We compare a model that conditions dispersal on geographical distance (D_{geo}) and on ecological resistance (D_{eco}) with the null model that assumes dispersal to be independent of any distance between regions (D_0).*

Model	AIC	delta-AIC
D_0 null model (no distance-dependency)	2693.8	51. 6
D_{geo} geographic distance model	2679.7	38.5
D_{eco} ecological resistance model	2641.2	0

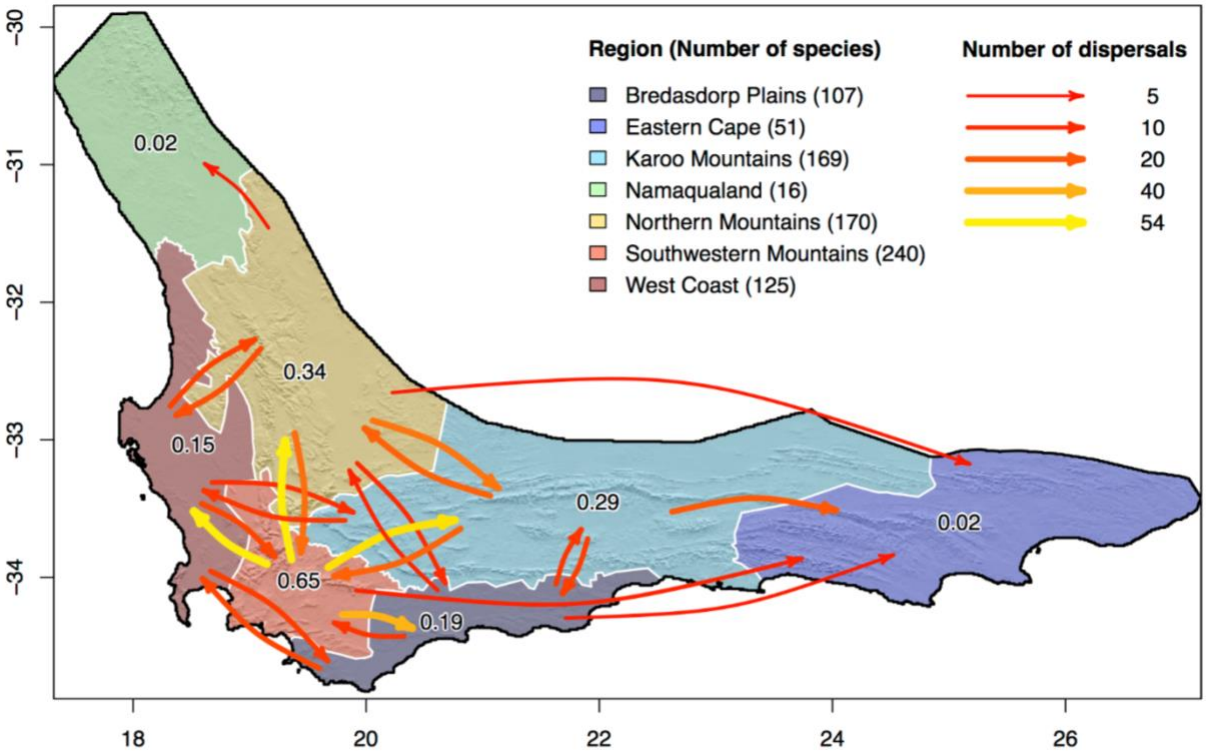

Figure 2 *The median number of dispersal events in restios among the regions in the Cape Floristic Region, calculated from the stochastic mapping repeats. Only reconstructions with more than four events are indicated, for details see Table S5. The number in each region is the proportion of in situ speciation, showing that the Southwestern Mountains have the largest proportion of in situ speciation, and are a net donor region.*

The number of dispersal events between regions was extremely high: across the 10,000 biogeographical stochastic mappings there were 557 (±76) dispersal events out of 634 branches in the restio phylogeny. As a result, in most regions the majority of the restio diversity was contributed by immigration rather than *in situ* speciation. The relative contribution of immigration still varied largely among regions, being highest in the Eastern Cape (0.98±0.02) and lowest in the Southwestern mountains (0.35±0.06). The relative contribution of *in situ* speciation also varied widely among regions (Fig. 2): from 0.65 (±0.06) in the Southwestern Mountains to 0.02 (±0.02) in the Eastern Cape. The region that exported most species to other regions was the Southwestern Mountains (214±19 spp.), whereas Namaqualand exported the fewest (6±4 spp., Table S5). Southwestern Mountains received most species from other regions (108±12 spp.), whereas Namaqualand received the fewest (18±7 spp.). The pairs of regions that exchanged most species were the Northern and the Southwestern Mountains (81±8 spp. exchanged in both ways), closely followed by the Southwestern Mountains and the West Coast (72±8 spp. exchanged in both ways; Fig. 2). All

other pairs of regions exchanged fewer than 51 species on average across stochastic mappings (Fig. 2).

Correlates of immigration and speciation

The proportion of immigration events that make up the diversity of each region is, contrary to our predictions, positively related to the degree of isolation (Fig. 3a, Table 3). However, as predicted, the proportion of immigration is lowest in the oldest regions, and highest in the youngest (Fig. 3b). The relative importance of *in situ* speciation in generating regional diversity shows a positive relationship to the area (Fig. 3c) and climatic heterogeneity (Fig. 3d) of the regions, and the explained variation is high (R^2 range from 0.50-0.84, Table 3).

Table 3 *Results from linear regression models testing the four biogeographical hypotheses to account for variation in regional richness of restios in the Cape flora. For each hypothesis, we report intercept and slope estimates (Estimate) together with their standard errors (Std. Error). We also report the models' R^2, together with its p-value. Note that we tested the first two hypotheses using the contribution of immigration (for isolation and age, leading us to expect negative slopes), whereas we used the contribution of speciation for the last two hypotheses (for size and heterogeneity, positive slopes expected). Also note that the significance threshold is set at α=0.0125 due to multiple testing.*

Hypothesis		Estimate	Std. Error	R^2	p
Isolation				0.53	0.063
	Intercept	0.1100	0.7878		
	Slope	178.3600	74.7286		
Age				0.84	0.004
	Intercept	6.8676	1.0677		
	Slope	-0.2086	0.0414		
Size (area)				0.63	0.032
	Intercept	-3.6091	0.7770		
	Slope	0.0004	0.0001		
Heterogeneity				0.50	0.074
	Intercept	-4.0373	1.1583		
	Slope	0.9863	0.4386		

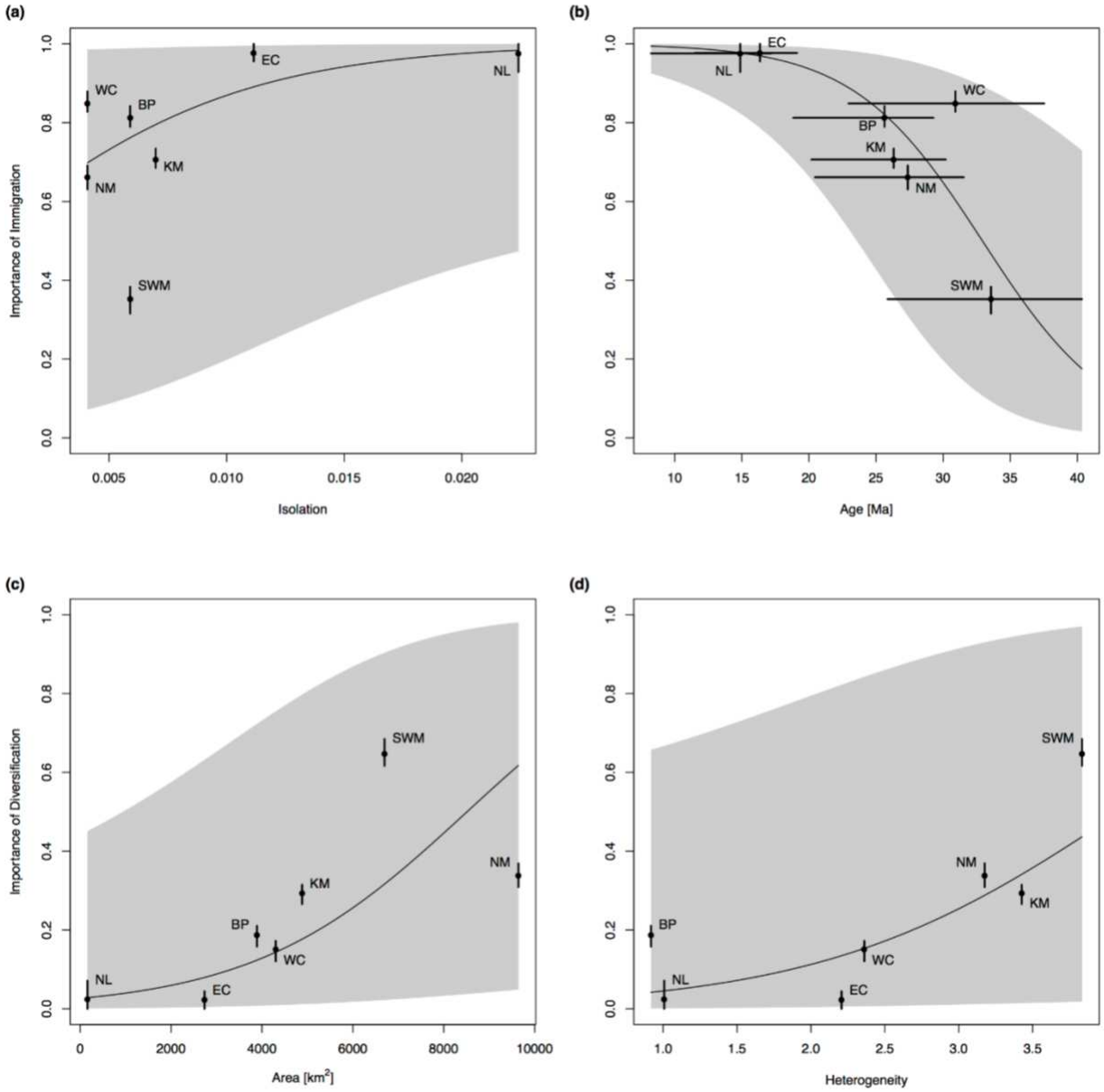

Figure 3 *The relative importance of immigration (a-b) or in-situ speciation (c-d) for restios in the Cape Floristic Region in relation to isolation (a), age (b), area (c) and environmental heterogeneity (d). Ranges on the y-axes (and x-axis in b) depict variation (inner quartile ranges) across the stochastic mapping repeats and the 100 phylogenetic trees. The black lines are predictions from the fitted models, with grey areas representing the prediction interval. Region abbreviations: BP (Bredasdorp Plains), EC (Eastern Cape), KM (Karoo Mountains), NL (Namaqualand), NM (Northern Mountains), SWM (Southwestern Mountains, WC (West Coast).*

DISCUSSION

We show that the suitable habitat of the fynbos (as exemplified by Restionaceae) is fragmented into regions separated by semi-permeable barriers, and the degree of permeability is best approximated by distance modulated by ecological suitability, rather than simple distance. The relative importance of *in situ* speciation is positively related to the area and heterogeneity of the environments in each region. The ancestral region, net donor of lineages, and area with highest *in situ* speciation, is the Southwestern Mountains. For all other regions the diversity is largely generated by immigration rather than *in situ* speciation.

Fragmentation is important

Our approach is built on the assumption that fragmentation among regions contributes more to turnover (and so potentially to differentiation) than simple distance. The long history of regionalization in the Cape flora (Linder & Mann, 1998; Linder, 2001; Moline & Linder, 2006; Oliver et al., 1983; Weimarck, 1941) suggests that distinct geographical regions, at least for restios, exist. This is corroborated by our demonstration that turnover is higher between, compared to within, the geographical regions. It has often been suggested that fragmentation increases diversity, for example in cushion plants of the Andes (Boucher, Lavergne, Basile, Choler, & Aubert, 2016). Fragmentation may influence diversification in several ways, either by increasing extinction or by stimulating vicariant and allopatric speciation. We demonstrate both a high dispersal rate across the barriers, as well as a significant effect of the barriers on compositional turnover. This is not consistent with the extinction model suggested by Brown (1971) for the sky islands in the Great Basin, where he argued that during the glacials a common fauna was distributed over all mountains, and that extinction, modulated by island size, drove the compositional differences among the sky islands. If the differences are the result of extinction, then isolation should have no impact, only area, and there should be no immigration between fragments. Levyns (1938) and Adamson (1958) suggested a vicariance model for the Cape flora, i.e. a once geographically continuous flora that is now restricted to montane climatic refugia and between which various plant lineages are diverging. Such vicariant speciation requires a relatively high level of isolation by barriers and not simply isolation by distance across a continuous extent of suitable habitat. The third model, allopatric speciation, possibly resulting from dispersal across semi-permeable barriers, has often been invoked for the Cape flora (reviewed by Goldblatt, 1978) and has been demonstrated for the sedge *Tetraria triangularis* species complex (Britton, Hedderson, & Verboom, 2014). This has been suggested to be general speciation model for the Cape flora (Verboom, Bergh, Haiden, Hoffmann, & Britton, 2015).

Heterogeneity and Area

Heterogeneity and area are highly, positively, correlated (R = 0.92), and both explain a substantial amount of the variation in the contribution of speciation to the regional species

richness in the restios. A potential role for environmental heterogeneity in driving the regional differences in species richness in the Cape flora was rejected by Cowling and Holmes (1992), on the argument that there was more heterogeneity in the species poor eastern than in the species rich western Cape. However, our results suggest the opposite, possibly due to a different definition of the regions. We do show a positive relationship: this could be simplified to the statement that the regions which include part of the coastal plain (Bredasdorp Plains, Namaqualand, West Coast, Eastern Cape) have a lower environmental heterogeneity, and lower species richness, than the more inland, mountainous, regions (Southwestern Mountains, Karoo Mountains, Northern Mountains). This coastal plain / mountains difference is consistent with the findings of Cowling and Lombard (2002) and Bouchenak-Khelladi and Linder (2017).

Barriers

Compared to most islands and isolated mountain systems (e.g., the sky islands in the Great Basin, or the tropic-alpine peaks of East Africa) the intervals between the Cape fynbos flora regions are very narrow, between 5 and 200 km. Our results show that even narrow barriers, in 10's of km, can be important. The Cape barriers are a complex combination of climatic and edaphic factors. Generally, the climates in the intermontane valleys, which constitute most of the barriers, are hotter and drier than the average fynbos climates (Campbell, 1983; Deacon, Jury, & Ellis, 1992). Edaphic factors are thought to be important in the Cape flora, with fynbos largely absent from the finer-grained clay soils found in the dry intermontane valleys (Rebelo et al., 2006). There are several implications of primarily ecological barriers. First, ecological barriers illustrate the limits to ecological flexibility in restios and other fynbos clades: if plant niches were evolutionarily labile, then restios would also be able to grow in the areas which now constitute the barriers, thus on the finer-grained soils and in hotter and drier climates. Secondly, restios may be absent in areas that form barriers because of biotic interactions if competitors in these areas exhibit superior performance and prevent restios from persisting in these habitats. Thirdly and most importantly, climate change may strengthen or weaken the barriers, fynbos can grow on well-leached shale soils under high rainfall conditions (Rebelo et al., 2006). Namaqualand, which is now isolated, is modelled to have been connected to the Northern Mountains during the last glacial (Midgley, Hannah, Roberts, MacDonald, & Allsopp, 2001), due to higher rainfall. We modeled connectivity between different regions as constant through time and based on current ecological distances. This is most likely not a valid assumption, but we have no data to indicate how these barriers varied during the Plio-Pleistocene.

Immigration and diversification within the CFR

Our results show a continuum between the central Southwestern Mountain region as a cradle of diversity (high *in situ* speciation and net export of lineages), and the peripheral Namaqualand and Eastern Cape regions as sinks of diversity (low *in situ* speciation and net

import of lineages). The regions in between are intermediate between these two extremes. The high richness of the Southwestern Mountains aligns with theoretical work suggesting that central regions of an archipelago should accumulate the highest species richness (Gascuel et al., 2016). Furthermore, the fact that this region is the one with the highest relative contribution of speciation also supports theoretical arguments for a role of increasing age, area and heterogeneity in driving *in situ* speciation within a region (Losos & Schluter, 2000). Such a pattern of a diversity centre with dispersal outwards, while retaining a high local diversification, was also demonstrated for the Southern Hemisphere with Australia as a source (Crisp et al., 2009), for the Neotropics occupied from Amazonia (Antonelli et al., 2018), and for red algae in the Indo-Pacific, expanding outwards from the Indo-Malay Archipelago (Leliaert et al., 2018) and may be quite common. The implication is that the Southwestern Mountain region acted as central cradle for diversity that over time built up the exceptional CFR diversity, both by *in situ* speciation and by seeding lineages into neighbouring regions, as well as further afield to the whole African montane flora (Linder & Verboom, 2015).

The build-up of restio diversity in the peripheral regions of the CFR (Namaqualand and the Eastern Cape) does not conform to classic predictions from island biogeography theory: given that they are the most isolated from other regions suitable for restios, we would have expected their diversity to have assembled mostly through *in situ* speciation, yet they have a surprisingly low speciation fraction. Both regions were occupied more recently than the Southwestern Mountains, but have probably been occupied by restios since the middle Miocene, and 15 My is enough time for speciation to generate a high diversity. A possible explanation for the low importance of speciation in these regions is that both may have occasionally been climatically marginal for restios during the Pleistocene. The only evidence available is from the last glacial. For Namaqualand Midgley et al. (2001) showed, based on species distribution models and modelled Last Glacial Maximum (LGM) rainfall and consistent with the fossil pollen record, that the fynbos vegetation was much more extensive and was connected to the Northern Mountains and the West Coast. Consistent with this Chase and Meadows (2007) and Scott et al. (2012) suggested that the western part of the Cape was wetter during the last glacial and became drier and warmer at the beginning of the Holocene, with the implication that the present highly restricted occurrence of restios in Namaqualand on the Kamiesberg and the coastal sand plain may be relictual from a formerly much wider range. The eastern half of the CFR (Karoo Mountains, Bredasdorp Plains and Eastern Cape) was probably drier during the glacials, with a more restricted distribution of fynbos. Quick et al. (2016) reported a 140 ky core from Vankervelsvlei near Wilderness, showing that the last interglacial had a climate similar to the modern one, but that the early glacial was seasonally arid and the glacial maximum droughted, and summarized extensive supporting information from other sites in the eastern CFR.

The intermediate regions (West Coast, Northern Mountains, Karoo Mountains and Bredasdorp Plains) have an intermediate position along the source-sink continuum, with 15-34% of local diversity generated *in situ*. The highest *in situ* speciation in this group is from the Northern Mountains, which may have had a stable fynbos vegetation during the Pleistocene, as indicated by the pollen record of a set of hyrax middens from Katbakkies in the Northern Mountains, analysed by Chase et al. (2015), which, similar to the nearby Cederberg swamp site (Meadows & Sugden, 1991; Meadows & Sugden, 1993), shows no compositional change during the Holocene. Bredasdorp Plains and the Karoo Mountains have a lower proportion of *in situ* speciation, suggesting a more unstable environment. Although no climate proxies are available from the mountains, those from the foothills (Agulhas plain [Carr, Thomas, Bateman, Meadows, & Chase, 2006]; and Boomplaas near Oudtshoorn [Sealy, Lee-Thorp, Loftus, Faith, & Marean, 2016]) do indicate a drier or more seasonal glacial. In addition, during the glacials the Bredasdorp and Eastern Cape coastal plains were much wider.

Overall, our results support some key predictions from island biogeography and meta-population theories (Table 1): we show that both the area and heterogeneity of a given region, as well as its age, are positively correlated with the relative importance of *in situ* speciation in restios (Fig. 3). However, we did not find the expected increase in the relative importance of *in situ* speciation that is expected with increasing isolation from other suitable regions, possibly because of the confounding effect of past environmental stability in the CFR, which has been lowest in the most isolated regions. The species diversity patterns, with most species in the south-western mountains, and the peripheral mountains relatively species poor, are common across many Cape fynbos clades (Oliver, Rourke, & Linder, 1983). However, the hypothesis that the processes which we document here for the restios also apply to these clades has not yet been tested.

Conclusion

The Southwestern Mountain region, irrespective of its definition has long been known to be the diversity centre of fynbos clades (Cowling, Bradshaw, Colville, & Forest, 2017; Levyns, 1938, 1958; Manning & Goldblatt, 2012; Oliver et al., 1983). We show that this diversity, in restios, is largely due to *in situ* speciation, consistent with its age, size and heterogeneity. This diversity may have been able to persist, because (as Adamson, 1958; Cowling & Lombard, 2002; Cowling & Holmes, 1992 argued) the climate has been more stable during the Pleistocene than in the Eastern Cape. We argue that it has also been more stable than in the Northern Cape. The current diversity in the more peripheral regions is largely due to immigration, but the total diversity of the CFR restios, especially in the intermediate regions, is largely the result of backwards and forwards dispersal associated with *in situ* speciation, very similar to the model described for the Canary Islands (Price et al., 2018).

The central role of the Southwestern Mountains in generating restio diversity highlights an important aspect that is often overlooked when considering biodiversity centres: while such centres of diversity as a whole are by definition exceptionally species- and endemic-rich regions, they are usually not homogeneous and different sub-regions within a centre might dramatically differ in how their biota was assembled. In particular, while biodiversity hotspots will generally be sources of diversity for neighboring regions, source-sink dynamics likely exist within hotspots.

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DATA ACCESSIBILITY

The set of 100 dated phylogenetic trees, the occurrence data, all topographic, geologic and environmental GIS layers, as well as the habitat suitability map for restios will be available on the DRYAD digital repository upon acceptance of the manuscript (http://dx.doi.org/XXXX).

BIOSKETCH

Rafael O Wüest explores the generation, preservation, and future fate of the diverse facets of biodiversity. He assesses community structure and assembly, models diversity along environmental gradients, and analyses how evolution and biogeography contribute to shape biodiversity patterns across scales.

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